From the Department of Dental Medicine
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MASTICATORY FUNCTION IN PEOPLE WITH DENTAL IMPLANTS

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Karolinska Institutet

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The cover illustrates the temporal profile of human masseter muscle activity in the beginning of the masticatory sequence for the dentate (green curve) and implant participants (blue curve) while chewing on hard food (skillfully and kindly drawn by Lina Trulsson).

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to my warmhearted Greek family and most of all, my wife, Anastasia, and our children Maria, Michael and Dimitrios

ABSTRACT

In use, since the 1960´s, dental implants have been reported to allow chewing that is as efficient as with natural dentition. However, input from periodontal mechanoreceptors (PMRs) around the tooth is important for sensorimotor regulation of biting and chewing. Since there is no periodontal ligament between osseointegrated implants and the alveolar bone, there are no mechanoreceptors in close proximity and, consequently, for individuals with such implants the sensory information sent to the central nervous system concerning chewing forces should be different than with natural teeth. The present thesis was designed to characterize the regulation of mastication in individuals with bimaxillary implant-supported bridges and to compare this to chewing with natural teeth, in order to gain new insights into the role of PMRs in this connection.

In the first study participants with natural dentition or fixed bimaxillary implant-supported prostheses chewed and swallowed two model foods of differing hardness while the electromyographic activity of the jaw-closing muscles and the position of the mandible were monitored. Those with implants exhibited impaired sensory-motor regulation during chewing, with less elevation of jaw muscle activity in response to hard food and attenuated adaptation of this activity as the masticatory sequence progressed. Next, we characterized the temporal profile of masseter muscle activity during natural chewing by young adults and the influence of food hardness on this profile. The excitatory drive of the masseter muscle was found to be biphasic, demonstrating an early component prior to tooth-food contact and a late component during this contact. To test our hypothesis that sensory input from the PMRs is required to achieve this later increase we finally investigated the effects of the absence of sensory input from PMRs in subjects with fixed bimaxillary implant-supported prostheses on activation of the masseter muscle during the jaw-closing phase of a chewing cycle.

Dentate participants exhibited a biphasic muscle drive during jaw-closing and throughout the masticatory sequence, with a component that starts just before the jaw-closing phase and is based on information from preceding chewing cycles, with no need for input from PMRs; and a late component that starts upon contact with the food, which is signaled by the PMRs. In contrast, participants with dental implants showed no such biphasic drive in the beginning of the masticatory sequence.

Adaptation of muscle activity during jaw-closing by the latter appeared to involve modifying the rate of the early component; while the more pronounced adaptation by dentate individuals seemed to reflect additional modification of the late, post-contact component, presumably in response to signals from the PMRs. However, later during the masticatory sequence, implant participants did show a biphasic drive during jaw-closing, probably achieved by prediction based on the gradually changing properties of the bolus during chewing. Moreover, the temporal profile of muscle activity during chewing was the same regardless of the hardness of the food.

In conclusion, sensory information provided by the PMRs appears to be most critical during the beginning of the masticatory sequence, when initial food contact occurs, whereas prediction of food properties based on information from other mechanoreceptors is utilized more effectively later on.

LIST OF SCIENTIFIC PAPERS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I. Adaptability of mastication in people with implant-supported bridges
Grigoriadis A, Johansson RS and Trulsson M
J Clin Periodontol. 2011;38:395–404

II. Temporal profile and amplitude of human masseter muscle activity is adapted to food properties during individual chewing cycles
Grigoriadis A, Johansson RS and Trulsson M
J Oral Rehabil. 2014;41:367-373

III. The temporal profile of masseter muscle activity during individual chewing cycles in people with dental implants
Grigoriadis A and Trulsson M
Manuscript

CONTENTS

LIST OF ABBREVIATIONS

AMA	Additional muscle activity
ANOVA	Analysis of variance
CNS	Central nervous system
CPG	Central pattern generator
EMG	Electromyography
FMR	Facilitatory masseteric response
N	Newton
PMR	Periodontal mechanoreceptor
r.m.s	Root mean squared
TMJ	Temporomandibular joint
VAS	Visual Analogue Scale

1 INTRODUCTION

When transforming an item of food into a bolus that is appropriate for swallowing, the masticatory system relies on information supplied continuously by various sensory receptors. The kinematics of the jaw and chewing forces must be adapted to the changing physical characteristics of the food. In this context a central pattern generator (CPG) in the brainstem rhythmically excites certain motor neurons, while simultaneously depressing others to control the depressor and elevator muscles of the jaw (Dellow and Lund, 1991). At the same time, as the properties of the food are modified during the masticatory sequence, sensory signals from receptors in the temporomandibular joints, mucosa of the oral cavity, and facial skin and lips; muscle spindles in the jaw muscles; and periodontal mechanoreceptors (PMRs) around the teeth allow continuous adaptation of the motor output (Thexton et al. 1980, Lund 1991, Thexton and Hiiemae 1997, Peyron et al. 1997, 2002, Woda et al. 2006, Westberg et al. 2011). For regulating the jaw-closing muscles during mastication, the latter two peripheral inputs are most important (Morimoto et al. 1989, Morimoto and Nagashima 1989).

With dental implants there is no periodontal ligament between the implant and the alveolar bone (so-called osseointegration) and thus no mechanoreceptors in close proximity (Klineberg et al. 2005, Trulsson 2006a). Consequently, the sensory information sent to the brain in response to chewing forces applied to a dental implant or natural tooth differs. Nevertheless, numerous studies have shown that rehabilitation with dental implants results in considerable improvement of function and comfort and these have been used successfully in the clinic since the 1960´s (Brånemark et al. 1969, 1977, Adell et al. 1970, Haraldson et al. 1977, 1979a b, Lundqvist et al. 1983, Lindqvist and Carlsson 1985, Haraldson and Zarb 1988, Jemt et al. 1988, Lundqvist and Haraldson 1992). Furthermore, chewing with an implant-supported prosthesis has been reported to be as efficient as with natural dentition, with similar maximal biting forces (Haraldson et al. 1977, Haraldson et al. 1979 a b c d, Adel et al. 1981, Haraldson and Zarb 1988). However, an interesting investigation by Haraldson (1983) suggested that regulation of jaw muscle activity during chewing with dental implants is impaired, indicating that the sensorimotor regulation of mastication is altered.

The present thesis was designed to characterize the regulation of mastication in individuals with bimaxillary implant-supported bridges. Since such individuals lack PMRs, a comparison to chewing with natural teeth will provide fundamental insights into the role of these receptors in this connection.

1.1 THE MUSCLES INVOLVED IN MASTICATION

The motor units through which the nervous system controls the contractile activity of muscles consist of a number of muscle fibers spread over a wide area, but innervated by a single motor neuron (α-motoneuron). The number of muscle fibers in one such unit varies from several to hundreds. Muscle fibers are classified into three types: the slow (S) fibers are highly resistant to fatigue; the fast-fatigable (FF) produce large forces rapidly, but only for a very short period; and the properties of the fatigue-resistant (FR) fibers are a mixture of those

of the other two. The slow fibers are recruited first; then the fast-resistant fibers; and, when sudden large force is required, the fast-fatigable. Motoneurons regulate muscle activity either by increasing the frequency of firing and/or through activation of additional motoneurons, thereby recruiting more motor units (see Loeb and Ghez 2000, Miles 2004a).

During mastication, four major pairs of muscles -- the temporalis, masseter, lateral pterygoid and medial pterygoid -- all innervated from the mandibular division of the trigeminal nerve (fifth cranial nerve), work together to create a bolus that can be swallowed.

1.1.1 The temporal muscle

The temporal muscle is large and fan-shaped; originates from the pterygoid fossa; passes the zygomatic arch; and forms a tendon that inserts into the coronoid process and anterior border of the ascending ramus. Elevation and retrusion of the mandible is determined by which of the three distinct areas of this muscle (the anterior, middle or posterior), with fibers in different directions, is activated. (Blanksma and van Eijden 1990, Tortora and Grabowski 1996, Okeson 2013).

1.1.2 The masseter muscle

Connecting the mandible with the zygomatic arch, the masseter muscle is described as having a superficial and a deep portion (Okeson 2013). The superficial portion arises from the anterior two-thirds of the zygomatic arch and contains a thick, multivariate aponeurosis that inserts into the angle of the mandible anterior of the ascending ramus. Underneath, the deep region arises from the lower surface of the zygomatic arch and inserts into the central apart of the ascending ramus in the mandible (Tortora and Grabowski 1996). This structure allows quite different types of contraction: the superficial fibers assist in elevation, protrusion and contralateral movements; while the deep fibers produce elevation, retrusion and ipsilateral movements (Hannam 1994). The masseter is considered to be the main muscle that pulls the mandible forcefully upwards (Hannam 1994).

1.1.3 The medial pterygoid

Originating from the pterygoid fossa, the fibers of the medial pterygoid muscle pass downward, backward and outward to insert along the medial surface of the mandibular angle. The primary function of this muscle is to elevate the mandible, but it can also protrude the mandible and move it from side to side (Tortora and Grabowski 1996, Okeson 2013).

1.1.4 The lateral pterygoid muscle

The lateral pterygoid muscle consists of both an inferior and superior head, originating from the outer surface of the lateral pterygoid plate and the infratemporal surface of the greater sphenoid wing, respectively (Tortora and Grabowski 1996, Okeson 2013). The inferior head inserts into the neck of the condyle and the superior into the articular disc. During jaw opening, the inferior lateral pterygoid is active, whereas the superior is inactive, as are all other masticatory muscles. The superior pterygoid acts mainly during jaw-closing,

presumably positioning the condylar head and disc in this context. Together, these two heads can protract the mandible, open the mouth and move the mandible from side to side.

1.1.5 The digastric muscle

The posterior region of the digastric muscle originates from the mastoid notch; while the anterior belly originates at a fossa on the lingual surface of the mandible; and the fibers of both insert into the hyoid bone. The major function of this muscle is, together with the other suprahyoid muscles (the stylohyoid, geniohyoid and mylohyoid), to depress the mandible (Tortora and Grabowski 1996, Okeson 2013).

1.2 SENSORS INVOLVED IN MASTICATION

1.2.1 Muscle spindles

Embedded among the extrafusal muscle fibers of skeletal muscle and innervated by α-motoneurons lie the muscles spindles that detect changes in length. Each such spindle is composed of a number of intrafusal fibers encapsulated in connective tissue and aligned in parallel with the extrafusal fibers. Both types of intrafusal fibers, the nuclear chain and nuclear bag, are innervated by γ-motoneurons (Hulliger 1984, Miles 2004b). A third type of motoneuron, the β-motoneuron, innervates both the intrafusal and extrafusal fibers (Burke et al. 1973).

The center of the muscle spindles receives afferent innervation by what is said to be the primary endings (annulospiral endings) of large, myelinated nerve fibers (group Ia afferents). The secondary endings of smaller nerves (group II afferents) are located at the poles of the spindle (Hulliger 1984). In humans, jaw-closing muscles such as the masseter and temporalis contain such spindles, whereas the jaw-opening muscles do not (Kubota and Masegi 1977, Lennartsson 1979). Furthermore, these spindles in the jaw-closing muscles contain very large numbers of intrafusal fibers, which may reflect an important proprioceptive role in connection with jaw function (Eriksson et al. 1994). The afferents that innervate these receptors are connected to the central nervous system through cell bodies located in the trigeminal mesencephalic nucleus (Matthews 1976).

When a muscle is stretched, both the extrafusal and intrafusal fibers are elongated and sensory signals thereby sent to the CNS from both group Ia and II afferents. When α-motoneurons are stimulated, the extrafusal fibers contract, shortening the muscle and causing relaxation of the muscle spindles. To prevent total cessation of spindle activity during muscle contractions, activation of the gamma efferents stimulates the intrafusal fibers to contract at the same rate as the main muscle fibers, thus maintaining steady tension on the muscle spindle. This gamma effect can evoke afferent activity from the spindles even when muscles are contracted and in this way assist in maintaining contraction.

1.2.2 Golgi tendon organs

The collagen fibers that form the tendons contain mechanoreceptors that inform the CNS about relatively small changes in muscle tension. These mechanoreceptors, referred to as Golgi tendon organs, are innervated by branches of group Ib afferents and are sensitive to low forces, becoming saturated at higher forces (Jami 1992). Golgi tendon organs have been detected in the masseter and temporalis muscles of the cat (Lund et al. 1978), but not in humans, and not much is presently known about their contribution to mastication.

1.2.3 Mechanoreceptors in the temporomandibular joint (TMJ)

Among the receptors located in the capsule of the TMJ are free nerve endings, Vater-Pacini corpuscles, Golgi organs and Ruffini endings (Thilander 1961), all with cell bodies in the trigeminal ganglion (Lund and Matthews 1981). It was proposed some time ago that TMJ receptors contribute continuously to the control of jaw movements during mastication (Klineberg 1980, Lund and Matthews 1981). Today, it is generally accepted that these receptors are activated primarily in connection with extreme movements of the jaw, such as opening, protrusion and lateral excursion, and they are therefore believed to make only a limited contribution to normal masticatory behavior. It has been suggested that during mastication these receptors contribute instead to preventing dislocation of the joint (Sessle 2006).

1.2.4 Mechanoreceptors in the facial skin, lips and oral mucosa

In addition to being sensitive to external deformation of the oro-facial tissues, mechanoreceptors in the facial skin, lips and oral mucosa provide proprioceptive information in connection with speech and jaw movements (Johansson et al. 1988a b, Trulsson and Johansson 2002). The four types of mechanoreceptive afferents in the soft tissues of the face and mouth are similar to those in the human hand: fast-adapting type I (Meissner corpuscles), slowly adapting type I (Merkel´s disk) and II (Ruffini), and hair follicle afferents (Johansson et al. 1988a, Edin et al. 1995, Trulsson and Essick 1997, Trulsson and Johansson 2002). It is noteworthy that the fast-adapting type II (Pacini) afferent, which is common in other parts of the body, appears to be absent from the face and mouth (Johansson et al 1988a, Bukowska et al. 2009, Trulsson and Essick 2010). The type I receptors respond to small and distinct areas, while type II receptors provide input from larger and less distinct areas. During oro-facial movements, such as chewing and speech, these afferents signal contact between the lips, deformation of the skin and generation of air pressure for speaking (Johansson et al. 1988b).

1.2.5 Periodontal mechanoreceptors (PMRs)

The PMRs are located close to the roots of the teeth, signal information about loads on a tooth, and thereby play an important role in controlling the jaw muscles during biting and chewing (Lund 1991, Trulsson and Johansson 1996a, Türker and Jenkins 2000, Trulsson 2006, Westberg et al. 2011; see Fig. 1). These nerve endings are located between the collagen fibers in the periodontal ligament that attach the tooth to the alveolar bone (Cash and

Linden 1982, Byers 1985, Linden 1990), and with cell bodies in either the trigeminal ganglion or trigeminal mesencephalic nucleus (Beaudreau and Jerge 1968, Gottlieb et al. 1984). These two different locations might reflect different functional roles (Olsson and Westberg 1989).

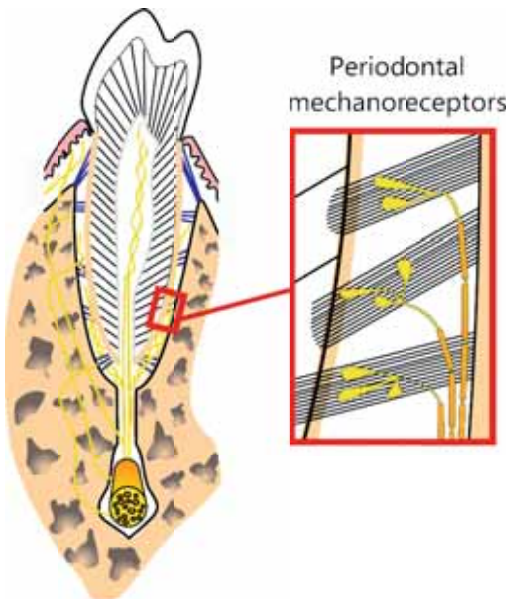

Figure 1. Periodontal mechanoreceptors are sensory organs located among the collagen fibers around the root of a tooth and signal information about loads on that tooth (modified from original artwork by Marie-Louise Rönnmark and Kurt Å Olsson, Umeå University, from Trulsson 2006b)

Although both free and a variety of more complex nerve endings have been described (cf Hannam 1982), the animal studies by Byers (1985) indicate that the PMRs are Ruffini in type, supplied by myelinated fibers and unencapsulated. Other investigators have confirmed the presence of 'Ruffini-like' endings close to these collagen fibers, both in animals (Byers et al. 1986, Byers and Dong 1989, Maeda et al. 1989, Kannari 1990. Kannari et al. 1991, Sato et al. 1992) and humans (Maeda et al. 1990, Lambrichts et al. 1992).

Microneurographic recording of signals from single human periodontal afferents has revealed that these provide temporal, spatial and force information about tooth loads (Trulsson et al. 1992, Trulsson 1993, Trulsson and Johansson 1994, Johnsen and Trulsson 2003, 2005). Human periodontal afferents generally adapt slowly, demonstrating both dynamic sensitivity to changes in force and static sensitivity to steady loads (Trulsson and Johansson 1996a). Together, groups of these afferents signal detailed information about the direction of forces applied to teeth, as well as about which tooth is loaded (Edin and Trulsson 1992, Trulsson 1993, Johnsen and Trulsson 2003).

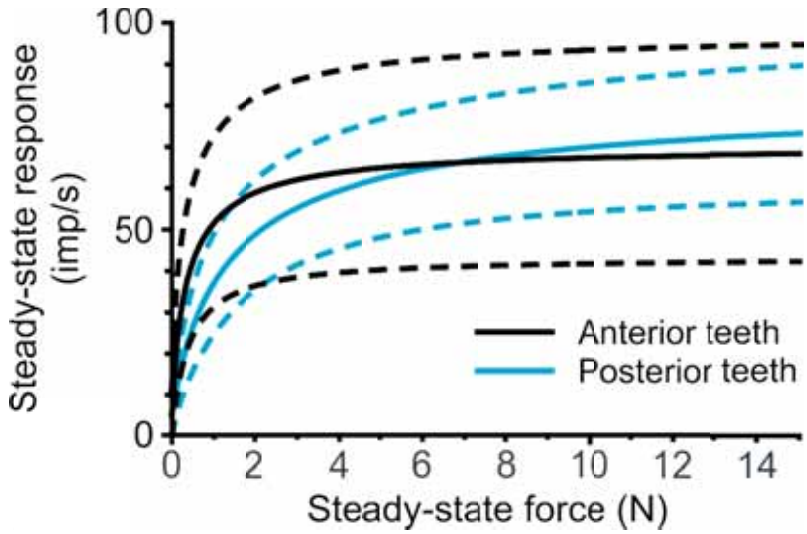

Figure 2. Steady-state stimulus-response relationship for periodontal afferents around anterior (black lines) and posterior (blue lines) teeth. The solid and dashed lines represent the mean values ± 1 SD, respectively, for 19 periodontal afferents around anterior teeth (Trulsson and Johansson 1994) and 20 periodontal afferents around posterior teeth (Johnsen and Trulsson 2005). Note the steeper curve at low force levels for the afferents around anterior teeth, indicating their higher sensitivity to low forces.

Most PMRs in the vicinity of both the anterior and posterior teeth exhibit pronounced saturation of their stimulus-response curve, with highest sensitivity to change at very low levels of force (see Fig. 2). The anterior teeth are most sensitive to changes in force below 1 N, while the posterior teeth are sensitive to changes in force as great as 3-4 N, with marked saturation at sustained forces above these limits in both cases (Trulsson and Johansson 1994, Johnsen and Trulsson 2005).

Simulations of the responses of periodontal afferents to chewing forces reveal that the rate of discharge by most PMRs increases rapidly upon initial contact between the tooth and food and the discharge then continues for as long as the tooth is loaded. However, due to the marked saturation, most of these discharges provide poor information about the magnitude of large chewing forces (Johnsen and Trulsson 2005). On the basis of such observations it has been hypothesized that shortly after tooth contact during each chewing cycle, the PMRs provide important input about the mechanical properties of food that can be used to prepare muscles appropriately for the upcoming power phase (Johnsen and Trulsson 2005, Trulsson 2006).

1.3 CONTROL OF MASTICATION

Early during the last century Sherrington (1917) noticed that stimulation of the oral mucosa of decerebrated cats evokes opening of the jaw followed by jaw-closing (the stretch reflex) and proposed that a series of jaw-opening and -closing reflexes are the basic masticatory movements. Much later, Lund and Dellow (1971) demonstrated that in decerebrated rabbits

masticatory movements are produced by a central pattern generator (CPG) located in the medial bulbar reticular formation situated between the motor root of the trigeminal nerve and the inferior olive. The CPG controls the basic rhythmical jaw movements by exciting certain motor neurons and simultaneously depressing others in the depressor and elevator muscles. Moreover, the CPG may also modulate reflexes by altering the excitability of interneurons in the pathways involved (Lund 1991). Although the basic rhythm is set by the CPG in this manner, control of mastication is achieved primarily on the basis of sensory feedback (Lund and Dellow 1971).

This has been illustrated clearly by experiments on rabbits (Appenteng et al. 1982, Lavigne et al. 1987, Inoue et al. 1989). During rhythmic chewing movements, the amplitude and duration of the masseter EMG normally rise when a steel ball or a thin plastic strip is placed between opposing molars (Lavigne et al. 1987, Inoue et al. 1989, Morimoto et al. 1989). However, removal of sensory feedback from the periodontal receptors by denervation (Lavigne et al. 1987, Inoue et al. 1989) or anesthesia (Morimoto et al. 1989) greatly attenuates such activation of the masseter muscle.

Furthermore, Morimoto and colleagues (1989) observed in rabbits that when the spindle cell bodies are destroyed by lesioning of the mesencephalic trigeminal nucleus, facilitation of the masseter muscle by application of the strip during cortically induced rhythmic jaw movements disappears almost completely (Morimoto et al. 1999). In addition, Hidaka and coworkers (1997) demonstrated that denervation of the maxillary and inferior alveolar nerves significantly reduces the rate at which force builds up during mastication. Thus, spindle afferents from the jaw-closing muscles, along with the PMRs play an important role in the regulation of mastication.

In humans, performing simulated chewing movements, only a fraction of the muscle activity observed is required to move the jaw, most of the ‘additional muscle activity’ (AMA) being needed to overcome the resistance of food (Ottenhoff et al. 1992a b). Such studies also suggest that the parameters for the AMA are set at least partially in advance on the basis of the food resistance detected during preceding cycles of chewing. This allows the build-up of adequate muscle force prior to tooth-food contact (feed-forward), with immediate modification in response to direct feedback from muscle spindles and PMRs concerning the forces acting on the teeth and muscle contraction. The cortex and other supra-medullary motor centers presumably play an important role in the feed-forward component (Westberg et al. 2011).

Indeed, this has been confirmed by observations that in anaesthetized rabbits chewing on a thin strip, ‘facilitatory masseteric responses’ (FMRs) often occur prior to teeth-strip contact during the second and subsequent masticatory cycles, but never during the first cycle. Furthermore, these FMRs are not altered by blocking the PMRs, but abolished by inhibiting the muscle spindles (Komuro et al. 2001a b), leading these authors to conclude that feed-forward control of the FMR depends primarily on sensory inputs from the latter. Interestingly, Johansson and Westling (1988) demonstrated a similar control mechanism in

the hand and arm during lifting tasks involving precision grip. Adaptation to the weight to be lifted is based primarily on information gathered during the previous lift, but if this is insufficient, the program is effectively updated on the basis of somatosensory inputs during the lift itself.

During mastication in humans, PMRs signal detailed information concerning the direction and point of attack of chewing forces (Trulsson et al. 1993, Johnsen and Trulsson 2003) that can be used by the CNS to adapt bite forces to the shape and location of the food (Trulsson and Johansson 1996a, Trulsson 2006). The significance of appropriate sensory information of this type is demonstrated clearly by the fact that individuals with a fixed bimaxillary implant-supported prosthesis exhibit obvious difficulties in performing the demanding task of splitting a spherical piece of candy into two parts of equal size between the front teeth, whereas subjects with natural dentition can easily perform a precise split (Svensson et al. 2011).

Microneurographic recordings and quantitative modeling have revealed that in humans the PMRs respond strongly at the time of initial tooth-food contact and are able to encode the low bite forces employed for holding and manipulating food (Trulsson and Johansson 1994, Johnsen and Trulsson 2005). Moreover, anesthetized subjects (Trulsson and Johansson 1996b) and subjects lacking PMRs (i.e. with a dental prosthesis or dental implants) (Trulsson and Gunne 1998) lack the fine motor control of low forces required to hold and split a morsel of food. The absence of information from the PMRs leads to higher and more variable forces when food is held and manipulated between either the anterior or posterior teeth (Trulsson and Johansson 1996a, Johnsen et al. 2007).

In addition to regulating relatively low holding forces via a feed-back mechanism, the PMRs also provide early information concerning the mechanical properties of the food that can be utilized in a feed-forward manner to adjust and adapt the motor programs controlling subsequent high biting forces. Accordingly, individuals who lack information from PMRs (anesthetized or with dental implants) cannot adapt the rate of increase in bite force to the hardness of food while splitting a morsel with the front teeth (Svensson and Trulsson 2009, 2011).

All in all, the sensitivity of the PMRs to initial tooth contact, the direction of forces and changes in low levels of forces indicate that these receptors play an important role in the sensorimotor control of mastication. Accordingly, lack of these receptors, as in individuals with a fixed bimaxillary implant-supported prosthesis, should be associated with disturbance of this control.

1.4 AIMS

1.4.1 General aim

The general aim of this thesis was to improve our understanding of the masticatory process in individuals with fixed bimaxillary implant-supported bridges. Since these individuals lack PMRs, comparison with chewing by natural teeth should provide insights into the role of PMRs in the sensorimotor regulation of natural chewing.

1.4.2 Specific aims

Study I

Here, we determined whether individuals with implant-supported bridges in both jaws can adapt the activity of jaw muscles to food hardness during mastication.

Study II

The temporal profile of activation of the masseter muscle in young adults during natural chewing was characterized, along with the influence of the hardness of the food on this profile.

Study III

Here, we investigated the effects of absence of sensory input from PMRs on activation of the masseter muscle during the jaw-closing phase of a chewing cycle.

2 METHODOLOGICAL CONSIDERATIONS

2.1 SUBJECTS

All participants in these studies were in good general health; none indicated any dental problems or dysfunctions with chewing; and all stated that they ate comfortably. Before participating, all subjects provided their written informed consent, in accordance with the Declaration of Helsinki.

Studies I and III

These investigations involved 8 men and 5 women (58 – 83 years of age; mean 71.1 years) with fixed full-arch prostheses supported by osseointegrated implants (Nobel Biocare AB, Sweden or Astra Tech AB, Sweden) in both jaws and 8 men and 5 women with natural dentition (59 – 79 years of age; mean 66.4 years). The participants with natural dentition had at least 28 permanent teeth and no apparent dental pathology. All of the participants with implants had had their prostheses for at least 12 months, with 6 supporting implants in the upper jaw in all cases and in the lower jaw, 4 supporting implants in 8 subjects and 5 in the remaining 5. All implanted prostheses extended to the second premolar or first molar region. All of the mandibular prostheses and 11 of the maxillary prostheses consisted of a metal frame to which acrylic prosthetic teeth were attached. In two maxillary prostheses, this frame was covered by porcelain. The most distal teeth in all prostheses had the size and shape of a molar. All participants exhibited normal occlusion.

Study II

Fourteen healthy participants (22 – 26 years of age, including 9 women) with natural dentition and at least 28 permanent teeth were included in this investigation. None had any known dental pathology or periodontal breakdown and none had undergone any type of endodontic, prosthetic or orthodontic treatment. Furthermore, none indicated any problems or dysfunctions with eating and all visited their dentists on a regular basis.

2.2 EXPERIMENTAL EQUIPMENT

Study I-III

Here, the three-dimensional movements of the lower jaw with reference to the upper jaw were monitored utilizing a custom-built apparatus (Umeå University, Physiology Section, IMB, Umeå, Sweden). In brief, employing dental composite cured by light, a small magnet (10 x 5 x 5 mm) was attached to the labial surfaces of the mandibular incisors. A lightweight frame attached to the head and equipped with an array of sensors (accuracy: 0.1 mm; bandwidth: DC – 100 Hz) tracked the position of this magnet in three dimensions. This frame rested on the upper part of the bridge of the nose and was fixed to the head by spectacle frames, the ends of which were joined by a strap around the head.

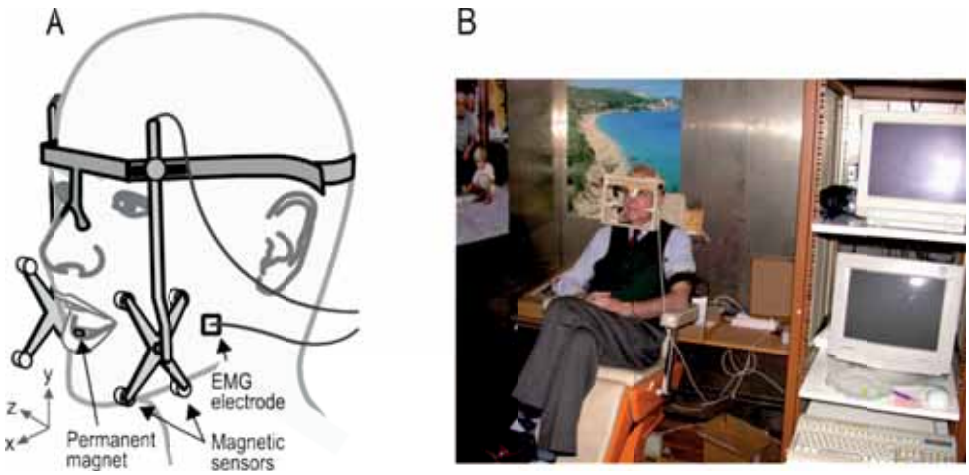

Figure 3. (**A**) Jaw movements were monitored by tracking the position of a small permanent magnet attached to the labial surfaces of the lower incisors, with magnetic sensors in a lightweight, head-mounted frame. Electromyographic (EMG) activity was recorded from the center of the masseter muscle using bipolar surface electrodes. (**B**) A subject sitting on a dental chair in a relaxed position while chewing model food during a trial.

This apparatus interfered minimally with oral functions and allowed normal movement of the head (Fig. 3). EMG signals were recorded bilaterally from the centers of the masseter and temporal muscles using bipolar surface electrodes (2 mm in diameter and 12 mm apart). During all experiments, we examined the EMG signals carefully for stability, stimulus artifacts, and noise.

2.3 SELECTION OF THE MODEL FOOD

Studies I-III

Masticatory behavior can be influenced by various properties of the food, including size, shape, and flavor (Woda et al. 2006). Most studies examining such effects have focused on the hardness of natural food (e.g., Agrawal 1998, Veyrune et al. 2007), even though hardness depends on a wide variety of factors, including brittleness, elasticity, plasticity, strength, toughness, viscoelasticity, and viscosity (see Foster et al. 2006) and such characteristics of natural foodstuffs are in general not well known (Woda et al. 2006). To get around this problem, viscoelastic model foods of controlled hardness and with well-defined physical (including rheological) properties have been developed (Lassauzay et al. 2000, Peyron et al. 2002, 2004).

Figure 4. The yellow (soft) and green (hard) visco-elastic model foods, identical in size (20 x 10 mm) and shape, but differing in hardness. Chewing of these model foods of specified hardness and with well-defined physical (including rheological) properties was monitored as illustrated in Figure 3. Here the small magnet (10 x 5 x 5 mm) attached to the labial surfaces of the mandibular incisors can also be seen.

For all three of our present studies, we prepared two visco-elastic model foods, identical in size and shape, but of differing hardness, in the manner described by Peyron et al. (2002). These foods were based on gelatin of two different grades and each item of food was 20 mm in diameter and 10 mm in height (Fig. 4).

A compressing machine (Autograph control/measuring unit, AG-G Shimadzu) was employed for duplicate determination of the mechanical properties of 10 samples from each batch of model food of each type.

2.4 EXPERIMENTAL PROCEDURES

Studies I and III

While sitting in a relaxed position in a dental chair (see fig. 3B), the participants chewed and swallowed 4 pieces each of the soft and hard model food, presented in an unpredictable order and without any information about their properties. First, the experimenter placed the model food on the extended tongue of the participant, hiding it from view to eliminate visual cues. The participants were instructed to hold the food between the tongue and palate with the mouth closed and teeth in the intercuspal position and 2-4 seconds after the food had been placed on the tongue, at a signal from the experimenter, to start chewing. Once done with chewing and swallowing, the subjects were instructed to return their jaw to the intercuspal position. They were free to drink, rest, speak and rinse out their mouths between trials. Before the trials, each was instructed to chew on the side he/she preferred (designated as the chewing side), if he/she had one.

The same experimental protocol was carried out on two separate days: the first time for familiarization with the general procedure, equipment and task; and the second as the actual test. After completing the chewing trials, the participants were asked to comment on whether they had experienced any problems and if the apparatus utilized might have disturbed their chewing. However, no questions concerning the properties of the food were posed.

After giving their answers, the participants chewed for 5 cycles on each type of model food, again in an unpredictable order, and rated its hardness on a Visual Analogue Scale (VAS, 100 mm) where 0 and 100 represented the softest and hardest food imaginable, respectively. Before spitting out the food into a bowl, they closed their eyes, again to eliminate visual cues.

Study II

This investigation was performed in the same manner as *Studies I* and *III*, except that the participants chewed and swallowed three pieces each of the soft and hard model foods on one occasion only. In addition, they were not asked to comment on their experience of the trial nor judge the hardness of the food.

2.5 DATA COLLECTION

In all three studies all signals were recorded, stored and analyzed using the SC/ZOOM microcomputer-based data acquisition and analysis system (SC/ZOOM, v.3.1.02, Umeå University, Physiology Section, IMB, Umeå, Sweden). The EMG signals were sampled at 3.2 kHz, while the vertical and lateral positions of the lower jaw with reference to the upper jaw were monitored at 800 Hz.

2.6 DATA ANALYSIS

2.6.1 Division of the masticatory sequence into segments and of the chewing cycle into phases

Our analysis focused on the average values for three consecutive chewing cycles at the beginning, middle and end of each masticatory sequence (Fig. 5A). The second to fourth cycles were defined as the beginning of the sequence; the second to fourth cycles before the final cycle as the end of the sequence; and the very first and last cycles were not analyzed because of their pronounced intra-individual variance between trials.

We defined a chewing cycle as consisting of an opening phase followed by closing and occlusal phases (Fig. 5B). For each participant, the occlusal state was defined as the minimal jaw opening (maximal jaw elevation) recorded during each trial, including when the participant first placed his/her teeth together in the intercuspal position. The opening phase ended with peak jaw-opening, when the closing phase accordingly began. The latter ended at the same vertical jaw position at which the opening phase began. Finally, the occlusal phase lasted from the end of the closing phase to the beginning of the subsequent opening phase.

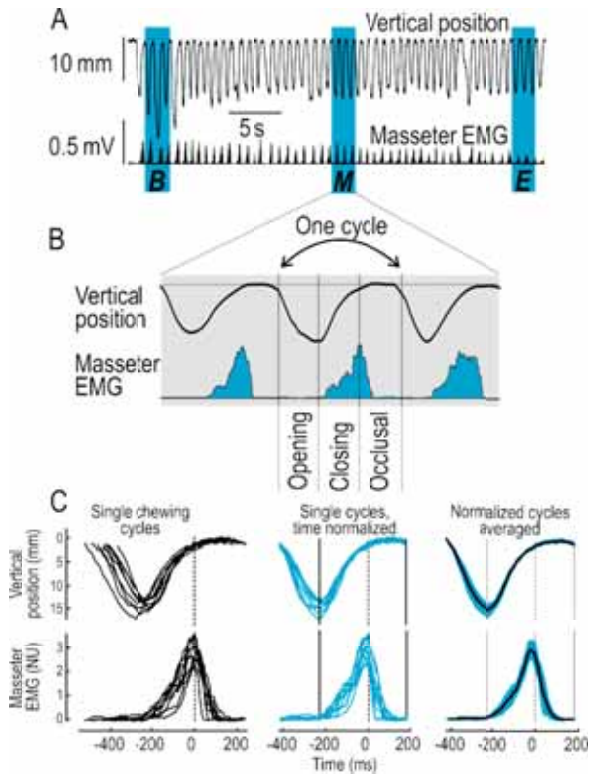

Figure 5. (**A**) The vertical position of the mandible and masseter EMG activity (root-mean-square processed) during a representative masticatory sequence. The blue boxes indicate the beginning (B), middle (M) and end (E) segments of the masticatory sequence. (**B**) A magnification of the middle segment illustrating the opening, closing and occlusal phases of a chewing cycle. The jaw-opening phase began when the jaw was opened from the occlusal state by 1 mm, ending at peak jaw-opening, and was followed by the closing phase that ended when the jaw had again reached the same vertical position as when the opening phase began. The occlusal phase began at the end of the closing phase and ended at the beginning of the opening phase of the subsequent chewing cycle. (**C**) Time-normalization of 9 chewing cycles (3 cycles during 3 masticatory sequences) at the beginning of the masticatory sequence for a participant chewing hard food. The values from these cycles, aligned at the onset of the occlusal phase (left panel), were normalized to (divided by) the mean duration of each of the phases (middle panel) and then averaged (right panel; mean ± SE).

2.6.2 Normalization of EMG signals

The EMG signals were processed by the root-mean-square (r.m.s.) procedure across a moving time window corresponding to ± 100 samples (±31 ms) and these signals then integrated for each phase of each chewing cycle, yielding a measure of the area under the processed EMG signal for each phase. In addition, the overall EMG signal for each chewing cycle was calculated as the sum of the integrated EMG signals for the three individual phases. To make the EMG data for the different participants comparable, for each participant, muscle, and phase of each chewing cycle, the integrated EMG activity was normalized to (i.e. divided by) the average total EMG activity of that same muscle during all chewing cycles

performed by the same participant. This normalization allowed us to examine the relative influence of type of food, segment of the masticatory sequence, and phase of the chewing cycle on the activity of each of the four muscles examined.

2.6.3 Normalization with respect to time

Studies II and III

To preserve temporal information that might otherwise have been lost by averaging temporal values for the different chewing cycles, the period of each phase in each cycle was normalized to the mean duration of that same phase during all corresponding cycles performed by all participants (Fig. 5C).

2.6.4 Parameters of jaw movement

Studies I and III

We extracted 10 values from the kinematic signals: for each trial, the duration of the masticatory sequence (from the start signal until swallowing) and the number of chewing cycles performed; and for each chewing cycle the durations of the entire cycle and of the jaw-opening and jaw-closing phases and the occlusal phase, as well as the peak-to-peak amplitude of vertical and lateral jaw movements and the peak vertical velocities of the jaw during its opening and closing phases.

Study II

For each chewing cycle, the duration of each of the three phases and the peak vertical amplitude and maximal closing velocity of the jaw were determined.

2.7 STATISTICAL ANALYSIS

We assessed differences between the dentate participants and those with implants using mixed-design ANOVAs, in which the data for the participants in each group are subjected to repeated measures analyses.

All ANOVA analyses were based on the mean values for each participant and combination of factors. A P-value of < 0.05 was considered to be statistically significant and we report all the significant main effects and significant interactions detected. Post-hoc comparisons were performed employing the Tukey HSD test.

2.8 ETHICAL APPROVAL

Study I was approved by the local ethics committee at Karolinska University Hospital in Huddinge, Sweden (Dnr: 04-715/4) and the regional ethical review board in Stockholm, Sweden (Dnr: 2009/1850-31/2).

Studies II and *III* were approved by the regional ethical review board in Stockholm, Sweden (Dnr: 2009/1850-31/2).

3 RESULTS AND DISCUSSION

For all participants the number of chewing cycles and duration of the masticatory sequence were greater with hard than with soft food (*Studies I and III*). With these two types of food the young participants chewed for 27 (±13.9; mean ± SD) and 21 cycles (±9.5), and 21.3 (±7.4) and 16.4 s (± 6.6), respectively (*Study II*). It has been demonstrated previously that individuals with removable prostheses supported by the oral mucosa use a greater number of chewing cycles of longer duration than those with natural teeth (Slagter et al. 1993, Veyrune et al. 2007, Mishellany-Detour et al. 2008). Here, the duration of the masticatory sequence and number of chewing cycles for dentate and implant participants were similar (*Study I*), indicating that chewing is less affected by implant-supported bridges than by removable prostheses.

3.1 DURATION AND PHASES OF THE CHEWING CYCLE

The duration of chewing cycles was not influenced noticeably by either the type of food (hard versus soft; *Studies I and II*) or the position of the cycle in the masticatory sequence (beginning, middle or end; *Study II*). Both the durations of the entire chewing cycles and their various phases differed between the dentate and implant groups (*Study I*). When chewing soft food, the duration of each chewing cycle was 0.80 ± 0.11 and 0.83 ± 0.16 s (mean ± SD) for these groups; and with hard food 0.79 ± 0.12 and 0.82 ± 0.17 s, respectively. For both groups the chewing cycle lasted longer as the masticatory sequence progressed: the average duration for both groups of participants and types of food was 0.73 ± 0.14, 0.76 ± 0.16 and 0.88 ± 0.25 s during the beginning, middle, and end of this sequence, respectively (*Study I*).

The durations of the opening, closing and occlusal phases of the chewing cycles did not differ between the dentate and implant participants ($p>0.05$ in all cases; *Study I*). Significant effects were observed for both the jaw-closing phase, which was shorter, and, in particular, the occlusal phase, the duration of which increased from an average of 0.27 ± 0.05 s in the beginning to 0.41 ± 0.17 s at the end of the sequence ($p<0.001$).

In the case of our young subjects, the duration of the opening and closing phases of the chewing cycle decreased ($p<0.01$ in both phases), whereas the occlusal phase became longer ($p<0.001$) as the masticatory sequence progressed (*Study II*). The hardness of the food exerted no main effect on the duration of any of the phases, but food and segment had an interactive effect on the duration of the opening phase ($p=0.01$), with only the hard food altering this duration during the masticatory sequence. Interestingly, the period during which the jaw-closing muscles were active corresponded to the combined duration of the closing and occlusal phases, neither of which was affected significantly by the nature of the food ($p=0.11$) or the time-point of occurrence of the chewing cycle in the masticatory sequence ($p=0.42$).

3.2 JAW MOVEMENTS

The amplitude of overall vertical jaw moment was larger with the hard than soft food (*Studies I and II*, see also Horio and Kawamura 1989, Agrawal et al. 1998, Lassauzay et al. 2000, Peyron et al. 2002, Foster et al. 2006) and declined as the masticatory sequence progressed ($p<0.001$ in all cases). However, during this sequence the implant participants did not adapt their jaw movements to the changing properties of the food to the same extent as the dentate participants ($p<0.05$; *Study I*). A post-hoc analysis revealed that hardness did not affect the vertical amplitude for the implant group significantly ($p=0.25$), but did so in the case of the dentate group ($p< 0.001$). Furthermore, as with the vertical movements, chewing hard food was associated with more pronounced lateral amplitudes than chewing soft food, irrespective of group (*Study I*; $p<0.001$).

As expected from the main effect of the hardness of the food on the amplitude of jaw movements, hardness also influenced the velocity of both jaw-opening and jaw-closing ($p<0.001$ in both instances), although this effect on jaw-closing was weaker and not statistically significant for the implant group ($p=0.38$ and $p<0.002$ for the implant and dentate groups, respectively; *Study I*). Moreover, both of these velocities declined as the masticatory sequence progressed ($p<0.001$ in both cases). However, this decline in the velocity of jaw-opening was less for the implant than the dentate group and in fact post-hoc analysis failed to indicate any significant effect in the case of the former group ($p>0.37$).

Altogether, the amplitude and velocity of mandibular movements by the dentate participants were elevated by food hardness (see also Horio and Kawamura 1989, Agrawal et al. 1998, Lassauzay et al. 2000, Peyron et al. 2002, Foster et al. 2006), whereas the participants with implants tended to use similar mandibular movements irrespective of the type of food (*Studies I and II*).

3.3 MUSCLE ACTIVITY

3.3.1 Amplitude of muscle activity

In agreement with previous reports (Horio and Kawamura 1989, Slagter et al. 1993, Feine et al. 1994, Hiiemae et al. 1996, Agrawal et al. 1998, Lassauzay et al. 2000, Peyron et al. 2002), in our investigations the EMG activity was greater when chewing on hard than soft food and this activity decreased adaptively as the properties of the food changed during the masticatory sequence (*Studies I-III*; $p<0.001$). The main reason for this decline was a reduction in muscle activity during the jaw-closing phase, whereas this activity during the occlusal phase either tended to increase (*Studies I and III*) or did not change significantly (*Study II*).

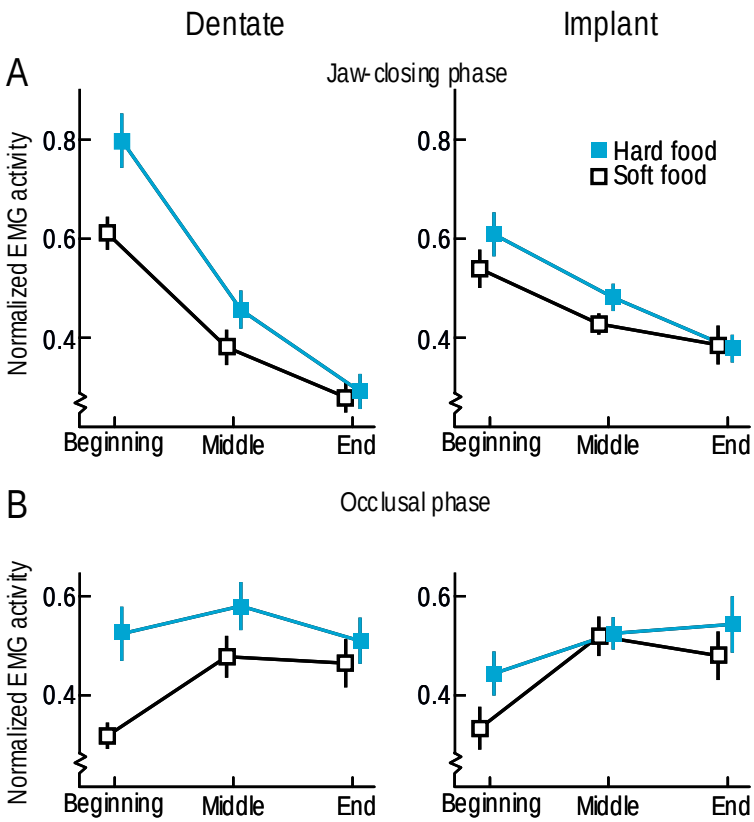

Figure 6. The average normalized EMG activity of all four muscles combined in dentate (left panels) and implant participants (right panels) during the three segments (beginning, middle, end) of the masticatory sequence when chewing on hard (blue) or soft (black) model foods. (**A**) The jaw-closing phase. (**B**) The occlusal phase. The symbols depict the average value of means computed for each participant and the error bars indicate the SEM (n = 13).

Although the chewing behavior of both groups was similar with the soft food, the participants with implants demonstrated an obviously impaired ability to adapt muscle activity while chewing the hard food (cf. the left and right panels in Fig. 6; $p<0.05$, *Study I*). The smaller decline in this case reflects primarily a less pronounced decline during the closing phases of the chewing cycle ($p<0.05$).

Furthermore, the difference in EMG activity while chewing hard or soft food decreased as the masticatory sequence progressed (Fig. 6; $p<0.001$), virtually disappearing for the closing phase by the end of this sequence (Fig. 6A).

During the masticatory sequence, the peak EMG activity was gradually reduced in size, particularly in the dentate groups ($p<0.05$; *Studies II and III;* see Fig. 7 and 8). Moreover, the temporal relationship of this peak to the onset of the occlusal phase shifted ($p<0.05$; *Studies II and III*), with no difference between the dentate and implant groups in this respect (*Study III*). For the dentate and implant groups, this peak preceded the onset of the occlusal phase by approximately 24 ± 4.6 and 17 ± 4.4 ms (mean ± SD) during the beginning cycles of chewing; and lagged behind this onset by approximately 16 ± 2.8 and 26 ± 3.5 ms in the middle and by 40 ± 2.9 and 36 ± 8.9 ms by the end, respectively. In the case of young subjects the peak EMG preceded the onset of the occlusal phase by 15.9 ± 13.2 and 13.8 ± 6.7 ms in the beginning and middle of the masticatory sequence, respectively, falling 20.3 ± 6.5 ms behind this onset by the end.

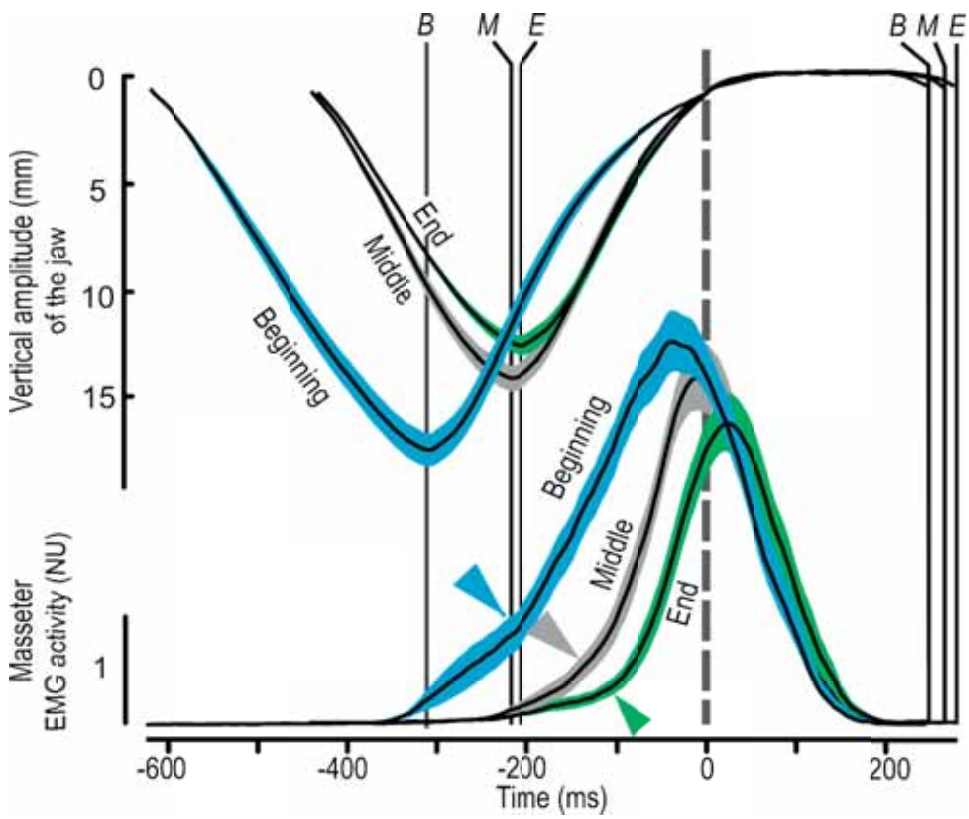

Figure 7. Vertical jaw movements (mm) and masseter EMG activity (in normalized units, NU) during single cycles of chewing on hard food. The values for all participants and chewing cycles were averaged normalizing the duration of each phase of each chewing cycle to the mean duration of that same phase for all participants. The data are aligned at the start of the occlusal phase (dashed vertical line at time 0) and the curves depict the mean values and the colored zones (blue=beginning; grey=middle; green=end) indicate ± SE (n=14). The vertical lines indicate the time of peak jaw-opening at the start of the closing phase and the end of the occlusal phase, for the beginning (**B**), middle (**M**) and the end (**E**) of the masticatory sequence. The arrowheads indicate the transition from the early to the late component of the increase in EMG activity during the closing phase.

3.3.2 The temporal profile of EMG signals during the jaw-closing phase

During mastication, both the dentate (*Study III*) and young subjects (*Study II*) exhibited a biphasic increase in the excitatory drive of the masseter muscle in connection with jaw-closing during the entire masticatory sequence (for the dentate and implant group, see the insets in Fig. 8). The early component, starting just before jaw-closing, involved moving the mandible to make contact with the food and generating bite forces (see Fig. 7 and 8). However, the implant participants only demonstrated a clearly biphasic muscle drive during the middle and end of the masticatory sequence (Fig. 8 B and C), i.e. early during mastication the subjects lacking PMRs failed to augment the increase in muscle activity at the end of the jaw-closing phase.

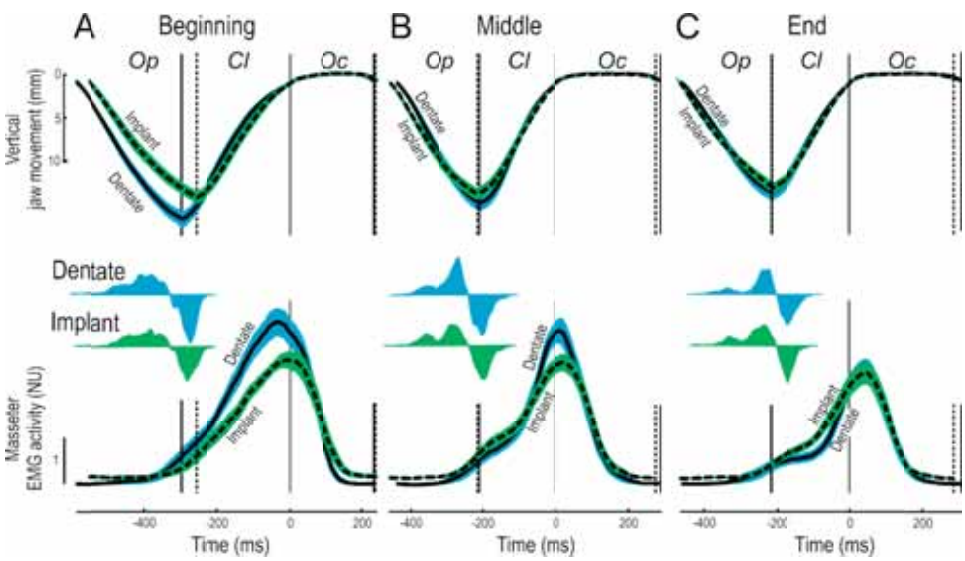

Figure 8. Vertical jaw movement (mm) and normalized masseter EMG activity (NU) for the dentate (solid curves with associated blue areas) and implant participants (dashed curves with green areas) during single cycles of chewing on hard food. The data for the beginning (**A**), middle (**B**) and end (**C**) of the masticatory sequence are averages for all participants and chewing cycles in each group (following normalization of the duration of each phase to the mean duration of that same phase for all participants in each group). The colored areas indicate the SE (n = 13) and the data have been aligned temporally to the start of the occlusal phase (time 0). The vertical lines to the left and right indicate the start of the closing phase (peak jaw-opening) and end of the occlusal phase, respectively. *Op*, *Cl* and *Oc* indicate the jaw-opening, jaw-closing and occlusal phases, respectively. The inset in the middle illustrates the rate of change in the average EMG signal.

Together with observations that blocking input from the PMRs by anaesthetizing rabbits significantly reduces the masticatory force during the "power phase" of the chewing cycles (Lavigne et al. 1987, Inoue et al. 1989, Hidaka et al. 1997), this lack of a distinct late component of muscle drive in the absence of PMRs indicates that information provided by

these receptors about tooth-food contact plays an important role in boosting the muscle drive to overcome food resistance. This impairment was also reflected in the finding that several of our implant participants failed to divide the morsels of food into several pieces even after five chewing cycles; whereas all dentate participants accomplished this successfully (Fig. 9). The reduction in jaw muscle activity as the masticatory sequence progressed occurred primarily during the jaw-closing phase and involved adaptation of both the early and late components (*Studies I-III*, see Fig. 7 and 8).

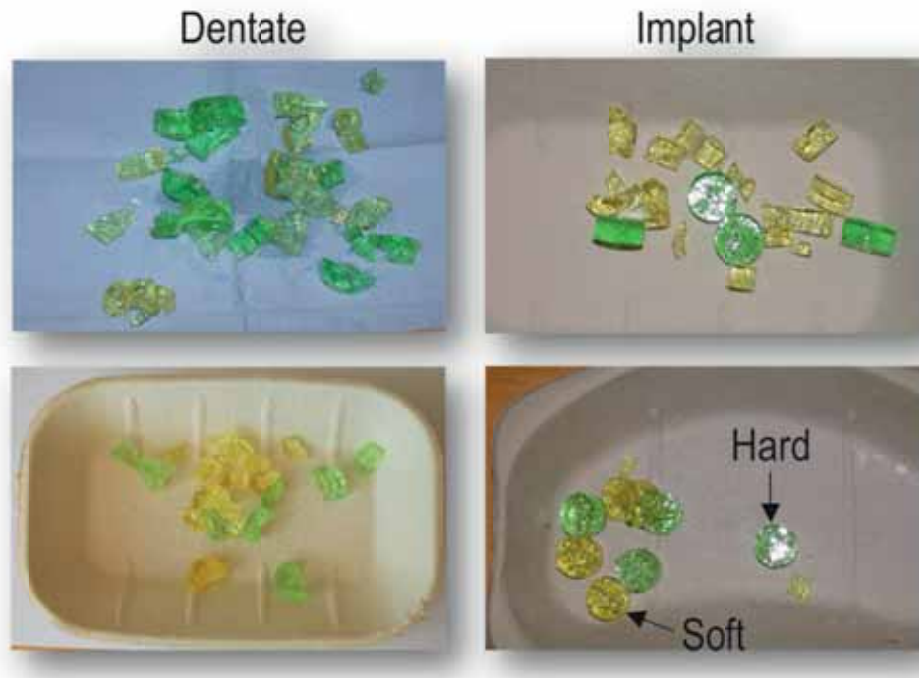

Figure 9. The effect of 5 chewing strokes by two dentate and two implant participants. The dentate participants successfully divided all of the morsels of food, irrespective of hardness, into several pieces. In contrast, the 2 implant participants failed to divide any of the hard (green) food and divided only half of the samples of soft (yellow) food into pieces.

It is noteworthy that despite their lack of a biphasic increase in the excitatory drive of the masseter muscle during jaw-closing in the beginning of the masticatory sequence, the participants with implants showed such a biphasic increase later on in this sequence. Probably, information about the properties of the food acquired during preceding cycles of chewing, in combination with a gradual change in these properties during successive cycles, allowed this predictive adaptation. In the absence of PMRs, the most important sensory information presumably originated from spindles in the muscles that close the jaw. Indeed, studies on animals have indicate that signals from muscle spindles are critical for feed-forward adaptation of a variety of facilitatory masseteric responses on the basis of information obtained during previous chewing cycles (Komuro et al. 2001a b).

3.3.3 The rate of increase in muscle activation

The rate of increase in muscle activation (reflected in the early component of the EMG) decreased gradually during the masticatory sequence (*Studies II and III*; $p<0.001$), with no difference between the dentate and implant participants in this respect (Fig. 8). For example, in young subjects, the peak rate was 10.6 ± 2.4, 5.6 ± 1.9 and 2.8 ± 1.2 NU/s (mean ± SD) in the beginning, middle and end of this sequence. Thus, reflected by the early EMG component of muscle activity, apparently accelerated prior to contact of the mandible with the food, thereafter reflecting the gradually declining acceleration of the mandible during jaw-closing as the masticatory sequence progressed ($p<0.01$; Fig. 7). In addition, the rate of muscle activation reflected in the late component of the EMG increased gradually during the masticatory sequence (*Studies II and III*; $p<0.01$), especially in the dentate group ($p<0.001$; Fig. 8B), regardless of food hardness and segment of the sequence.

Our observation that prior to the onset of tooth-food contact implant individuals adapts their muscles to the changing properties of the food in an appropriate manner indicates that information from the PMRs is not necessary for such regulation. This conclusion is in agreement with reports that in anaesthetized rabbits, the additional muscle activity (AMA) prior to food contact is unaffected by blocking the PMRs, but eliminated by impairing input from muscle spindles (Komuro et al. 2001a). Essentially, most of the adaptation of the EMG activity by our implant participants during the jaw-closing phase appears to result from adjusting the rate of increase in EMG prior to tooth-food contact. In contrast, the more robust and pronounced adaptation by dentate participants seems to reflect additional modification of the late, post-contact component, presumably in response to signals from the PMRs.

3.3.4 The point of transition between the early and late components of muscle activation

Interestingly, in the case of the dentate (*Study III*) and young participants (*Study II*) the transition between the early and late components of muscle activation during the jaw-closing phase appeared to occur at about the same time as contact with the food (both hard and soft). During the first segment of the masticatory sequence, this transition was estimated to occur when the jaw had opened approximately 11 (*Study II*) or 12 mm (*Study III*) for the young and dentate participants, respectively (see arrowheads in Fig. 7), which corresponds to the size of the model food. In contrast, due to their absence of a biphasic drive, implant participants showed no such transition point during the beginning of the masticatory sequence (see Fig. 8A).

As the size of the food particles was gradually reduced, the transition between the early and late components was associated with less and less opening of the jaw ($p<0.001$; *Studies II and III*; Fig. 7 and Fig. 8B and C). For the young subjects the corresponding jaw-opening during the middle and end of the masticatory sequence was 9.5 and 7.2 mm, respectively. The reduction in jaw-opening at the transition point was less for the implant (8.9 mm in the middle and 8.0 mm at the end) than for the dentate group (9.5 and 7.2 mm) ($p<0.001$).

In light of the pronounced sensitivity of PMRs to low contact forces (Trulsson and Johansson 1994, Johnsen and Trulsson 2005), signals provided by these mechanoreceptors may contribute to initiation of the late component. In humans performing simulated chewing, two complementary mechanisms appear to regulate generation of muscle activity to overcome the resistance of food (Ottenhoff et al. 1992a b): commands to the muscles are made in advance utilizing predictions of food resistance based on sensory input from preceding chewing cycles; and also modulated by immediate feedback from oral mechanoreceptors. With respect to the latter, animal studies suggest that signals from muscle spindles are most important during early jaw closure, whereas inputs from both muscle spindles and periodontal mechanoreceptors are important later on (Lavigne et al. 1987, Inoue et al. 1989, Morimoto et al. 1989, Komuro et al. 2001a b).

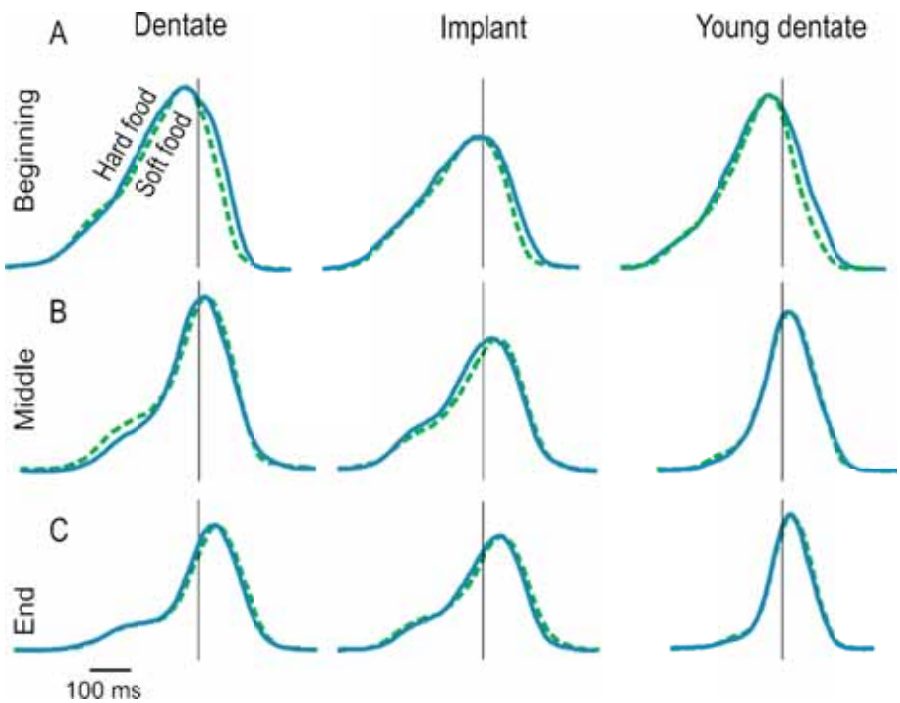

Figure 10. The mean activity of the masseter muscle (after normalization to peak amplitude) when chewing hard (solid blue curves) or soft food (dashed green curves) for all dentate, implant and young dentate participants. These data for the beginning (**A**), middle (**B**) and end (**C**) of the masticatory sequence are the averages for all participants and chewing cycles in each group and have been aligned to the start of the occlusal phase (time 0).

3.3.5 Effect of food hardness

Overall, the temporal profile of muscle activity (illustrated for the masseter muscle in Fig. 10) was virtually identical during natural chewing of hard or soft food (*Studies II and III*), indicating that the principal effect of food hardness was on the magnitude of activity. Furthermore, food hardness did not affect the timing of the peak EMG activity relative to the onset of the occlusal phase during any segment of the masticatory sequence ($p>0.05$ in each case).

4 CONCLUDING REMARKS

4.1 SUMMARY OF THE MAJOR FINDINGS

Haraldson (1983) proposed that patients with dental implants use the same muscle activity during the entire masticatory sequence. Here, we demonstrate that participants with a **bimaxillary implant-supported prosthesis** do, indeed, exhibit **impaired sensorimotor regulation** during chewing, with less elevation in jaw muscle activity in response to food hardness and attenuated adaptation of muscle activity as the masticatory sequence progresses.

Furthermore, our findings reveal that during the jaw-closing phase throughout the masticatory sequence, dentate participants show a biphasic muscle drive. **The early component** appears to move the mandible up to allow tooth-food contact; begins just before the jaw-closing phase; and is based on predictive information obtained from earlier chewing cycles, with no need for sensory input from the PMRs. Moreover, **the late component** starts when **tooth-food contact first occurs.**

In contrast, participants with **dental implants did not show** such a **biphasic muscle drive** in the beginning of the masticatory sequence, reflecting the difficulties they had in biting through the model food when chewing five times (see Fig. 9). Therefore, we propose that input from the **PMRs** in connection with tooth-food contact plays an **important role** in **boosting** the **muscle drive** in order to overcome food resistance. It is important to note that our participants with implants did show a biphasic increase later in the masticatory sequence. They were probably able to do this by **using information** about the food acquired from orofacial mechanoreceptors (most likely the **spindles** in the **jaw-closing muscles**) during the **previous chewing** cycles to **adapt** motor **commands** in a predictive manner.

All in all, adaptation of the EMG activity during the jaw-closing phase by individuals with **implants** appears to involve **modifying** the **rate** of the **early component**; while the more pronounced adaptation by **dentate** individuals seems to reflect additional **modification** of the late, **post-contact** component, presumably in response to signals from the PMRs.

Another central finding here was that the **hardness of food** does **not influence** the **temporal profile of muscle activity** during chewing, indicating that the primary effect of food hardness is on the amplitude of the EMG and is independent of the PMRs.

Sensory information concerning food contact provided by the PMRs appears to be **most critical** during the **beginning** of the masticatory sequence, when this contact first occurs. Assessment of food properties on the basis of signals from other mechanoreceptors can be achieved more effectively later during this sequence, when the properties of the bolus are changing only gradually during each successive chewing cycle. These conclusions are also supported by our unpublished findings on young subjects chewing visco-elastic model food with and without anaesthesia of the upper and lower teeth on the chewing side. When **anaesthetized**, in the absence of essential information from the PMRs, these subjects exhibited **impaired** adaptation of **muscle activity** to food hardness, **no longer** being able to

produce a **biphasic increase** in the excitatory drive of the masseter muscle in connection with jaw-closing during the beginning of the masticatory sequence (see Fig. 11A). In other words, they failed to generate a distinct augmentation of this drive when tooth-food contact occurred. Moreover, they were unable to enhance the activity of their jaw muscles in response to harder food to the same extent as without anaesthesia and their adaptation of muscle activity as the masticatory sequence progressed was poorer. In addition, several **anaesthetized** participants **failed** to **divide** most of the morsel of **food** into pieces with five chewing cycles (see Fig. 11B).

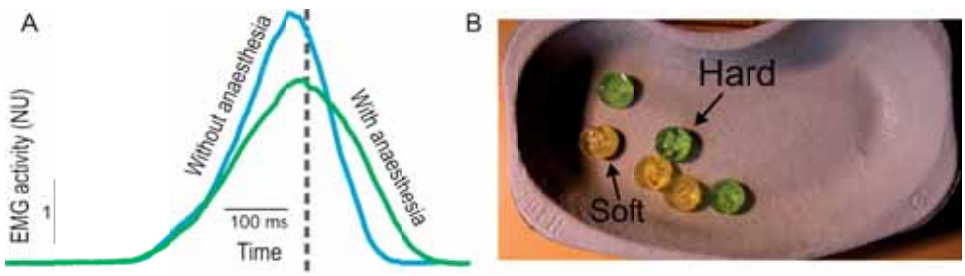

Figure 11. (**A**) Masseter EMG activity (in normalized units, NU) during single chewing cycles in the beginning of the masticatory sequence, for young participants chewing visco-elastic model food without (blue) and with (green) anaesthesia of the upper and lower teeth on the chewing side. These values are averages for all participants and chewing cycles. (**B**) After 5 chewing cycles, one anaesthetized participant failed to divide the morsel of either type (soft=yellow; hard=green) of food into pieces.

4.2 FUTURE PERSPECTIVES

Clearly, additional studies designed to improve our understanding of oral function in individuals with dental implants are required. At present, the anatomical and esthetic outcomes of prosthodontic treatment can be assessed in a satisfactory manner, but objective evaluation of masticatory function is not yet clinically possible. The patient can be asked questions about perceived function, but interpreting the answers properly is a challenge, considering that the patients that are totally edentulous have gone from having a removable prosthesis with varying success to a fixed implant prosthesis.

When an amputee receives a leg prosthesis, a team of doctors, physiotherapists, and other specialists begin a comprehensive training program designed to achieve as much independence as possible, so that the patient can live an active life. Following major prosthetic dental treatments we lack such rehabilitation programs.

During the VAS trials, we noticed that approximately one-third of the participants with a bimaxillary implant-supported prosthesis had severe problems in dividing the morsel of food into pieces with five chewing cycles, whereas the others performed well. We hypothesize that certain patients retained the previous chewing behavior they developed with removable upper and lower prostheses and were unable to adapt to more stable, fixed, implant-supported

prostheses. Therefore, in the near future we intend to initiate studies on sensorimotor re-learning by patients who receive dental implants, with the goal of improving their masticatory function. Patients with implant-supported prostheses in both jaws and obvious problems in chewing hard food into pieces will be recruited.

The outcome of such investigations on re-learning will aid in the development of novel clinical approaches and effective routines for rehabilitation of masticatory function. The development of such routines will certainly improve the benefit patients receive from dental implants.

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